Report   Charles R.C. Sheppard, Mark Spalding, Clare Bradshaw and Simon Wilson

Erosion *vs.* Recovery of Coral Reefs after 1998 El Niño: Chagos Reefs, Indian Ocean

Three years after most corals died on the central Indian Ocean reefs of Chagos, erosion and recovery were studied to 30 m depth. Mortality was near-total to 15 m deep in northern atolls, and to > 35 m in central and southern atolls. Some reef surfaces have 'dropped' 1.5 m due to the loss of dense coral thickets. Coral bioerosion is substantial, reducing 3-D reef 'structure' and forming unconsolidated rubble. Juvenile corals are abundant, though mostly on eroding or unstable substrates, and are of less robust species. Reef fish abundance and diversity at 15 m depth remains high; species dependent on corals have diminished, while some herbivores and detritivores have increased. A new sea surface temperature (SST) data set shows that mean SST has risen 0.65°C since 1950. The critical SST causing the mortality in Chagos was 29.9°C.

INTRODUCTION

After the 1998 rise in sea-surface temperature (SST) caused massive coral mortality throughout the Indian Ocean (1), scientists were asked two main questions: how quickly will reefs recover or erode, and what would the costs and consequences be to local communities? Most island archipelagos were severely affected, with mortality of over 90% to considerable depths in the Maldives, Seychelles and Chagos (2–4). Some places escaped, such as Mauritius, where cloud shielded the island for the critical period (5), and the northern Red Sea, but the geographical extent of the mortality was great.

In the Chagos Archipelago (Fig. 1), a snorkelling survey in 1999 confirmed that mortality was almost total to 10 m depth

(4). Air temperature patterns (6) showed a rise of about 1°C over 25 yrs, with a corresponding reduction in cloud and an increase in wind variance. At that time no sea-temperature series were available.

Following the 1998 event, it was predicted that significant changes could take place to the reefs of all affected areas, including Chagos (1). Many corals killed were hundreds of years old, and it was clear that, whether or not the cause was 'cyclical' or even 'natural', an event of this magnitude had not occurred for several centuries, or even millennia (7).

As well as having great intrinsic interest, the Chagos archipelago is an important stepping stone in East-West migrations of marine species in the Indian Ocean (8). Belying its small island area (4000 ha), its reef habitat to 60 m depth is ~13 000 km^2 (9), giving it enormous biogeographical importance.

This survey determined patterns of benthic mortality, erosion and recruitment of new corals, and examined reef fish communities, comparing the results with premortality data. Net reef growth is a balance of erosion, coral growth, and of poorly quantified factors which stabilize and cement coral sand and rubble. The nature and stability of the substrate is crucial; coral larvae preferentially settle on encrusting calcareous algae (10, 11), where mobile rubble can quickly kill them. This paper assesses the present balance between erosion and new growth.

METHODS

Elevated SST was the main cause of coral mortality in the Indian Ocean in 1998. A new compilation of 'HADISST data' (12), provided monthly SST readings centered on Chagos, from 1950, in 9 cells of 1° lat. and long.

Covers by coral and soft coral were measured to 30 m depth using line intercept transects, in the same sites measured in all previous surveys in Chagos since 1979 (13, 14). This was supplemented by visual estimates of cover; where both were done together, eye estimates were < 5% different from cover estimates obtained from transects. Also a 10 m tape was laid horizontally at 12 m depth at each site, and the maximum dimension (to 1 cm) and gross morphology (branching coral, table coral, unidentifiable) of every piece of rubble over 1 cm underlying the tape was recorded. Pieces of branching coral rubble (7–10 cm long) were collected and examined for bioerosion (15). Each piece was split 5 times and bioerosion was estimated on a 3-point scale (< 33%, 33–66%, > 66%). Pieces were selected from patches near recently killed coral heads in an attempt to standardize fragment ages. This was repeated at intervals of 100 m. Additional fragments which were completely encrusted with calcareous algae were collected for comparison. At Diego Garcia atoll, bioerosion in rubble was also compared with that of *in situ* dead table coral. Chi-squared tests and correlation analyses were used to analyze geographical patterns of amount and type of erosion.

The 3-D relief (rugosity) of the reef surface was quantified with the chain method. A light chain is laid over contours of the substrate, and the ratio of the planar distance to the length of chain gives a measure of rugosity (16). This was standardized to 10 m lengths.

Densities and sizes (between 2–160 mm) of young corals were counted in 25 x 25 cm quadrats, from which their ages were inferred (17). Surviving patches of living tissue from older colo-
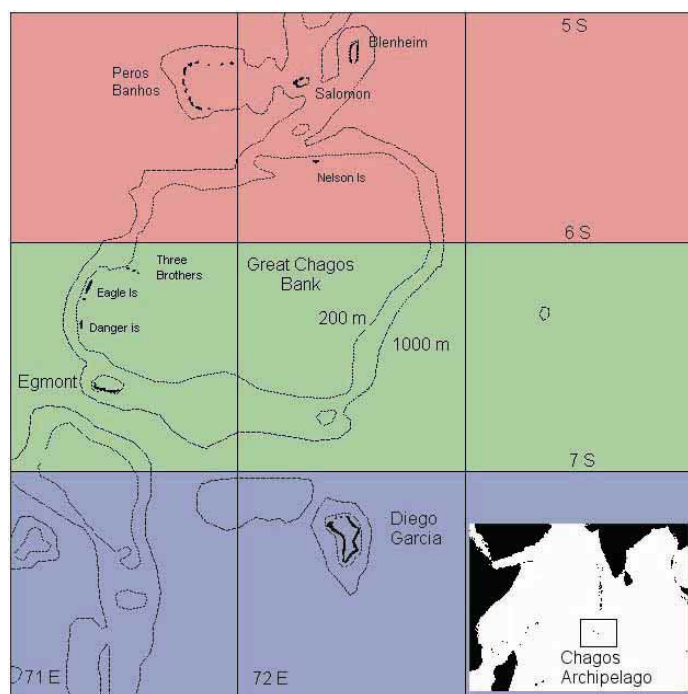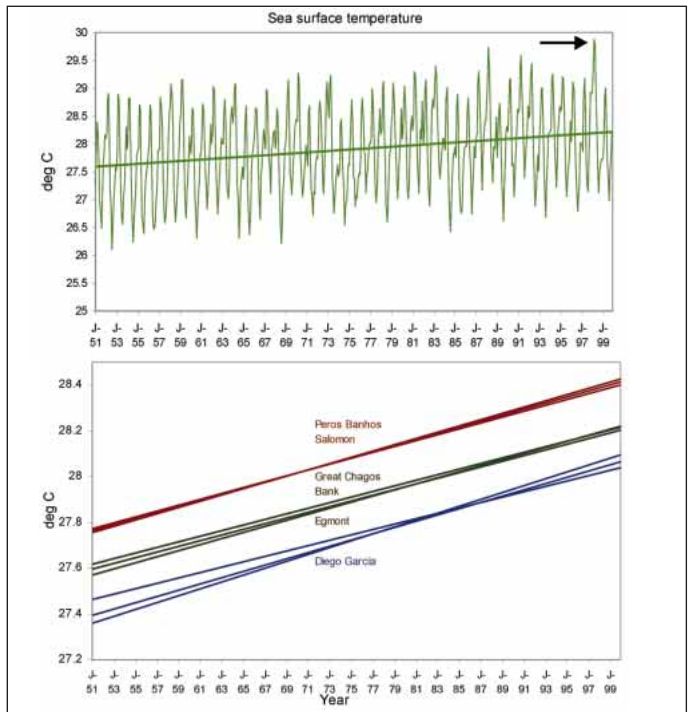
Figure 2. Top: Monthly mean sea temperatures of the middle row of latitude (including much of Great Chagos Bank and Egmont atoll). Straight line is the simple regression line. Arrow marks the point which caused the 1998 mortality.
Bottom: Simple regression lines for all 9 cells. All individual points removed for clarity. 'J' on x-axes indicates January.

nies were excluded. Juveniles were counted on substrate categories termed Bare Coral Rock, Rubble, *in situ Acropora* tables, other *in situ* branching colonies, and Consolidated Rubble. Quadrats were sampled randomly, but any with more than one substrate type or mature coral colonies were rejected.

Reef fish were counted in an underwater visual census in 10-m diameter fixed plots over 20-min periods. Repeated counts (6 on outer reef slopes, 4 in lagoons) were combined to characterize each site (18). Five sites were examined, 4 on seaward reefs censused at 15 m depth, and a fifth on a group of lagoon reefs in Peros Banhos atoll at 10-m depth. Species lists were also compiled which included semiquantitative abundance estimates for each species.

RESULTS

Surface Seawater Temperature Changes

SST showed a consistent rise in all 9 cells (Fig. 2). Annual variation is ~ 3°C. Mean temperature rose over 50 yrs by nearly 0.7°C or about one quarter of the magnitude of an annual cycle. Lines of best fit show rises of near perfect consistency, with warmer cells (red) nearest the equator, and cooler cells (blue) further south. In all cells, peak monthly temperature was 29.9°C, in April 1998. For the northern 6 cells this was the highest ever recorded, though for the southernmost row of 3, 1 month in 1988 was similarly warm. Air and SST track each other closely (12); air temperature is cooler by 1–2°C, but is rising faster. The higher specific heat capacity of water explains this difference, but acceleration of SST rise seems possible.

Critical SST values for coral mortality vary according to region (19). In Chagos, 29.9°C is a key indicator of coral mortality, providing a useful index for prediction of future similar events, though factors such as UV penetration are also important. Simple extrapolation of these data, not shown, suggests that the straight-line rise in April SST will reach this critical value in about 2020, and even mean annual SST will do so in 2030. Annual fluctuations above this 'lethal index' may occur repeatedly well before that time, and indeed nearly did in April 2001 (19).

Coral Cover and Reef Condition

In shallow water, there is substantial erosion and removal of dead colonies, and large numbers of new, small juveniles. Erosion of dead corals was marked. Less than a third remained of the previously dominant 'finger corals'; skeletons were usually covered in thick, encrusting red algae. Where the large *Acropora palifera* used to dominate on north-west facing reefs, the killed colonies have been almost totally removed. Since these used to form a 1–2 m tall, impenetrable thicket to about 5-m deep, their removal has effectively lowered parts of these reef surfaces by about 1 to 2 m (Fig. 3).

Previously, between 6 to 15 m, there were numerous table corals. Their condition in 2001 varied. In several locations, all tables had been removed, and with most boulder corals also dead the substrate was now becoming featureless (Fig. 4). This region, just shallower than the reef 'drop-off', previously had the highest coral diversity with over 200 species (13). Here, surface features of most boulder corals have eroded, and diversity of survivors is low. Coral cover in most sites shallower than about 10–

Figure 3. Dead *Acropora palifera* colonies *in situ*, 2–5 m water depth. The dead colony used to be surrounded by others, densely packed. Dead *A. palifera* colony, demonstrating vertical extent of dead stump = 1.5 m. Note small living *Acropora* near base.

Figure 4. Typical condition in 2001 of seaward reef slopes, 5–15 m deep particularly in central and southern atolls. Mounds are all dead eroding corals, with some stumps of table corals. Some encrusting soft coral regrowth visible. Live coral cover at these sites was < 1%, compared to > 60% in 1996.

15 m was < 10%, the remainder being expanses of bare limestone. In many sites, upright skeletons of tables were abundant below 6-m depth, their eroding and fragile tops providing important, temporary habitat for juveniles (see later and Fig. 10)

There was a marked geographical pattern of mortality (Fig. 5). The northern atolls Salomon, Blenheim and Peros Banhos were much less affected below 12–15 m depth where cover rose significantly (r = 0.532, p < 0.01). However, coral cover in these areas is also greatly reduced compared with 22 yrs ago (Fig. 6); their vibrant appearance is in part merely a contrast with elsewhere. Sites near lagoon passes, and occasional unusual sites carpeted with the coral *Echinopora lamellosa*, increased the overall visual richness of these northern sites, which are likely to be most important for future recovery.

Further south, severe mortality continued to at least 30–35 m depth. At 4 seaward sites, 3-D relief increased with depth of water; reef surfaces are now fairly smooth in shallow water, becoming more structurally complex with depth.

Soft-coral cover remains < 5% at most sites, though several genera show recovery between 10–20 m depth, from almost zero in 1999. The large, bushy and black ahermatypic coral *Tubastraea micrantha* was conspicuous in the southernmost atoll Diego Garcia, along with numerous sea-whips. This is explained by persistently observed cold thermoclines at 10–15 m depth at that southern atoll. Reef building coral now has very low cover to at least 30 m depth on Diego Garcia's western, seaward side.

Lagoon sites generally had greater relief than outer slopes, and greater survival of large colonies. Many parts of the lagoons have

lost most corals and soft corals, but relatively rich patches still occur. Most notable were examples of large, living *Acropora*, including tables 1.5 m diameter, something not seen on seaward slopes. In general, corals in areas of restricted water circulation survived better; one explanation is that they may be adapted to regular warming of their waters.

Erosion and Rubble

Rubble was extremely abundant (Fig. 7) though disintegration is not uniform across the archipelago (Table 1). Most rubble pieces were smaller than 15 cm, with mean sizes 3–6 cm, but in some exposed sites mean rubble size was only 2.97 cm, (s.d. 1.73). At some locations, chutes of scoured substrate indicated that much rubble is now being carried into deeper water.

Correlation analysis (Table 2) showed significant relationships between rubble size with latitude and longitude. The western edge of the Chagos Bank has smaller rubble, suggesting a more advanced state of erosion. Standard deviations of mean rubble size also correlate with latitude and longitude. Superimposed on

Figure 6. Coral cover with depth in northern atolls (those least affected by 1998 mortality) in 2001. Top pair of lines (dotted) are 1979. Bottom pair (solid) are 2001. Top of each pair is corals + soft corals, bottom of each pair, corals only. All 4 curves are second-order polynomials (hence the 'cross-over' at left of bottom pair is an artefact).
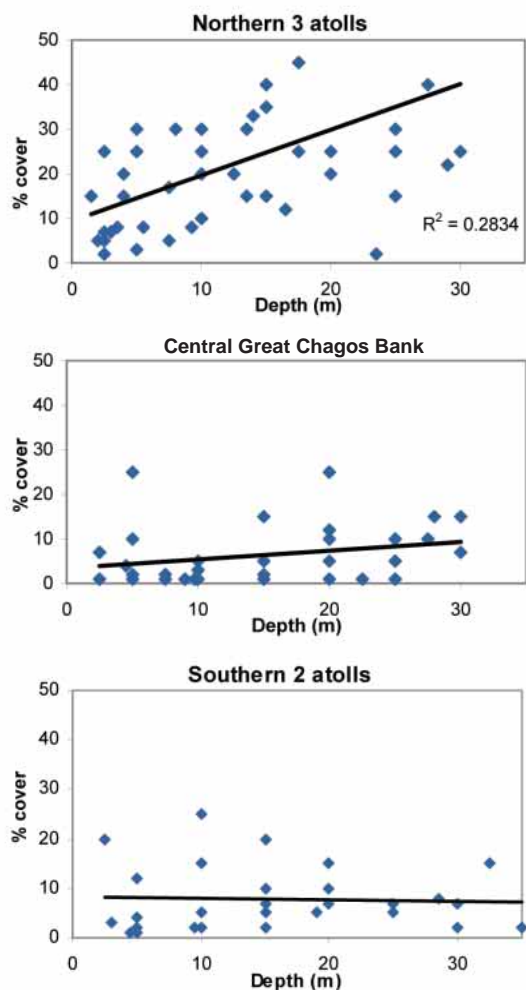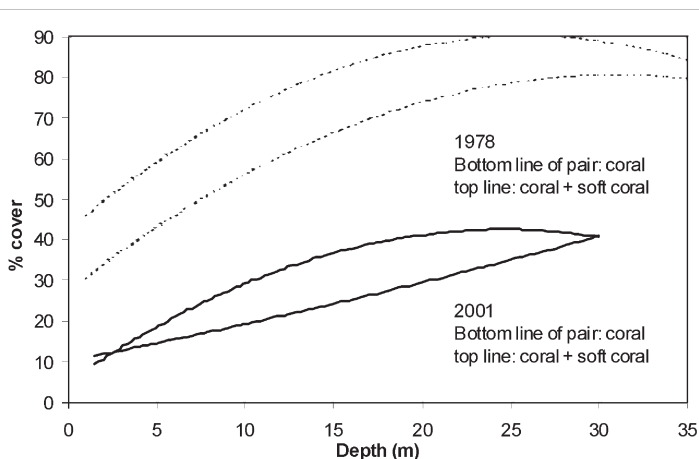

Figure 5. Geographical pattern of coral cover with depth on seaward reef slopes. Data pooled by atoll: 8 transects on northern 3 atolls, 7 transects from central regions, and 5 transects from southern atolls. Northern atolls: r = 0.532, significant trend with depth (p = 0.01). In middle and southern sites, r is not significant.

Figure 7. Typical rubble formed from disintegrating fragments of coral colonies.
Top: Rubble with less encrusting red algae; pieces are more brittle and tunnelled.
Bottom: Cross sections of coral fragments illustrating bioerosion scores of 2 or 3.

this, however, is atoll size: smaller rubble (more advanced erosion) occurs in larger atolls, and at 2 sheltered lagoonal sites rubble was larger with a wider range of sizes.

Infestation by biota in rubble is not related to size or location of the atoll (Tables 1, 2). Bioerosion of all rubble was high (present in 94% of all split surfaces). Sponges were the most abundant bioeroders, (81% of split surfaces), followed by various worms (57%). Most split surfaces (56%) showed less than 33% cavities formed by bioerosion (score 1 in Table 1), while < 10% of rubble had > 66% removed (score 3).

Within each atoll, bioerosion was fairly consistent, although outer slopes tended to have a little less. Heavy encrustation with coralline algae did not offer protection from bioerosion. On seaward reefs sponges are the primary agent. Lagoons showed the same amount, though the main eroders in Salomon lagoon were algae (> 85% of samples), which were absent from all seaward sites. Lagoons had more worm eroders (~ 75%), and were more affected by external bioerosion, mainly parrotfish scrapes. To depths of 3–5 m, the bioeroding sea urchin *Echinothrix* sp. was locally very abundant, often in dense clusters of 100 individuals. Scrapes by feeding parrot fish occurred on all types of substrate, including new coral recruits. In 0–6 m, a black boring sponge was common in reef pavement, visible as a series of black spots flush with the reef rock, forming patches up to several meters in diameter. At Diego Garcia, *in situ* coral was much less affected than loose rubble, and had fewer parrotfish scrapes.

These patterns reveal something about erosion processes since 1998. Breakdown of rubble depends on rates of fragmentation,

Table 1. Summary of data for each site. Bioerosion scores: 1 = 0–33%, 2 = 34–66%, 3 = > 67%. N = number of sites from which collection was made. (C= rubble covered with calcareous algae, T = covered with 'turf'. 'as above' refers to rubble size / rugosity figures for Peros Banhos further up the Table. Bioerosion scores: 1 = 0–33%, 2 = 34–66%, 3 = > 67%.

| | Rubble | | | | Bioerosion | | | | | | |
| | | | | | score frequencies (%) | | | Bioerosion | % | % | S:W |
Island	N	mean	s.d.	mode	1	2	3	score	sponge	worm	ratio
Nelson	–	–	–	–	–	–	–	–	69.57	44.93	1.55
Salomon	6	6.84	5.42	4	63.17	24.13	12.70	149.52	87.92	57.25	1.54
Blenheim	4	10.46	8.44	5	68.03	23.77	8.20	140.16	72.22	67.98	1.06
Peros Banhos	9	5.84	5.55	2	68.88	24.77	6.34	137.46	75.16	58.25	1.29
Middle Brother	2	3.95	3.06	1	52.00	35.00	13.00	161.00	89.00	66.00	1.35
Eagle Island	2	4.12	3.57	2	56.47	34.12	9.41	152.94	87.75	62.25	1.41
Egmont	3	3.57	2.58	4	56.00	31.33	12.67	156.67	80.00	48.00	1.67
Diego Garcia	2	6.67	6.07	4	42.67	36.00	21.33	178.67	93.33	89.33	1.04
Ile Poule (C)					82.86	11.43	5.71	122.86	60.00	57.14	1.05
Lagoon (C)	as	above			56.00	36.00	8.00	152.00	76.00	64.00	1.19
Lagoon (T)					68.00	28.00	4.00	136.00	64.00	64.00	1.00

Table 2. Results of correlation analyses testing the relationship between rubble size, bioerosion and island position and size.
Blank cells = no relationship. % coral with sponge and % coral with worm are the % of split surfaces in which this biota was present.

| island data | | | rubble size | | | rugosity | | | bioerosion | | | | | |
atoll area (km²)	lat (S)	long (E)	mean	s.d.	mode	mean	% corals with sponge	% corals with worm	sponge: worm ratio	% corals with < 33% with erosion	% corals with > 66% erosion	total score	
	(**)	* –	* –							* –			atoll area (km²)
		** –	** –	** –						** –	** +	** +	lat. (S)
		** +	** +	** +									long. (E)
			(**)	(**)	** –							** –	mean rubble
			(**)	** –						* +			s.d. rubble
			(*)										mode rubble
				** –		* +							mean rugosity
						(*)				* +	* +		% coral with sponge
						(**)							% coral with worm
													sponge worm ratio
										** –	(**)		% corals with < 33% erosion
											(**)		% corals with > 66% erosion
													total score

KEY

*	slight relationship (significant at p = 0.1)
**	relationship significant (p = 0.05)
– or +	direction of relationship
( )	meaningless/biased comparison

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export and accretion. Some rubble pre-dates that event, although selection of pieces from patches derived from recently collapsed colonies reduced this error. The coral species, size, shape and density are important, and bioerosion is faster in shallow water. However, to standardize as much as possible, depth of sampling was always 12 m except at some lagoonal sites, and coral fragments were only taken from the reef surface. Bioerosion accelerates once the coral starts to fragment, and breakdown has been faster in the south of the region. Corals still *in situ* tend to be encrusted with algae and invertebrates which may protect them from bioeroders (Fig. 7). However, once they break off and are loose on the seabed, these 'protective' species do not survive, and bioeroders dominate.

Breakdown has been very rapid at most sites, leaving rubble which is small and loose, with little consolidation after 3 yrs into a firm framework on which new coral recruits can thrive. On the other hand, continuing removal of large amounts of dead coral is tending to leave bare rock that is often covered in crustose coralline algae, which provides good potential substrate for new coral settlement.

New Coral Recruitment

The proportions of each measured substrate type varied with depth (Fig. 8). Most substrate types have restricted depth distributions; only 'coral rock' extended over the full range. A total of 1147 juveniles was measured and identified in 235 quadrats at 20 sites. Average density of juveniles was 4.88 quadrat^{-1}, equivalent to 78 corals m^{-2}, and the mode was 2 juveniles quadrat^{-1}, equivalent to 32 corals m^{-2}.

Twenty-five scleractinian genera and 2 hydrozoan genera (*Millepora* and *Heliopora*) were encountered. *Acropora* was most common (n (individuals) = 317), followed by *Montipora* (n = 194), *Pavona* (n = 132), all Faviids (n = 104) and *Porites*

(n = 86), together accounting for 76% of juveniles. The genera *Leptastrea, Psammocora, Coscinaraea, Pocillopora* and *Cyphastrea*, were each encountered 20–50 times. Together these account for 93% of all juveniles; 17 further genera account for the remainder. The rate of encounter of new genera shows that they are most often found early at a new site, causing a stepped 'discovery curve' (Fig. 9), which strongly suggests that sampling captures most groups likely to occur at a site, while the stepped shape of the curve indicates patchiness of coral recruitment.

In situ Acropora tables attracted significantly more recruits than any other substrate (Table 3, Fig. 10); there were no sig-

Figure 10. Dead *Acropora* tables. Pie chart: average proportions of space occupancy on 30 seaward slope table corals from 8-15 m depth. The area marked 'bare' area is in fact covered by films of microscopic and tiny filamentous algae. Photos: examples of *Acropora* tables in varying stages of disintegration. Top: Numerous juvenile corals (mainly *Acropora*) on tables. Bottom: Eroding edges clearly visible; filamentous green and especially red algae cover much of the remaining surface.

Figure 8. Relative proportions of the 4 substrate types with depth, based on quadrats sampled. Note particularly the distribution of dead *Acropora* tables.
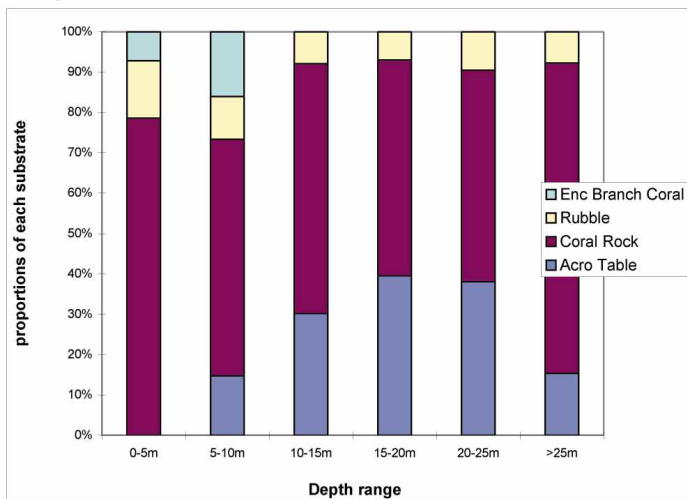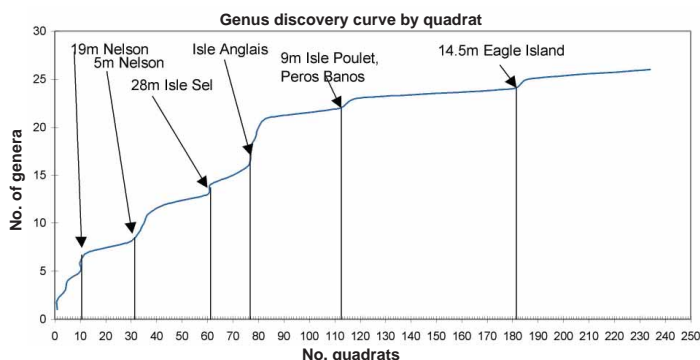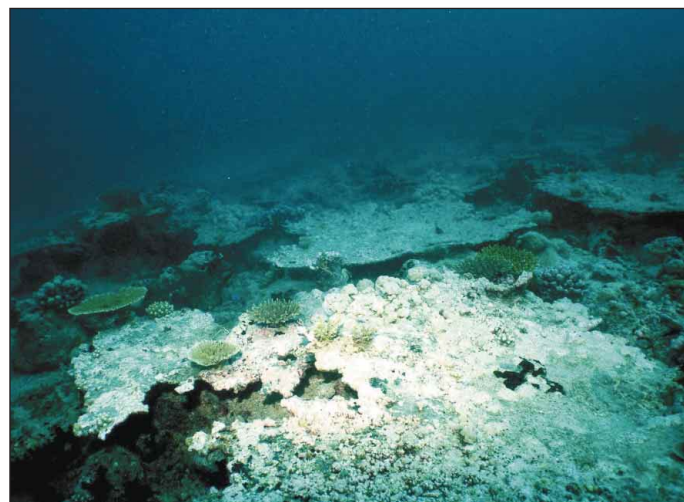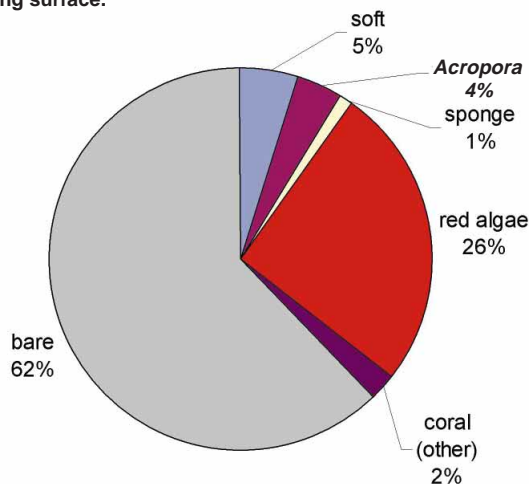

Figure 9. Genus 'discovery' curve of juveniles from all quadrat data.

nificant differences in recruitment pattern between any other substrate type. Most recruits on dead coral tables were themselves *Acropora* juveniles. No such differences were detected in other genera. There appeared to be no significant effect on density by depth over the depth range of 0–30 m (χ^2-Test; p = 0.91).

Table 3. Mean density of recruits (per 625 cm^2 quadrat) on different substrates. The last column is calculated to permit regional comparisons.

	Average	s.d	*Acropora* juveniles	s.d	N	Average per m^2
In situ Acropora tables	6.93	6.27	5.29	3.86	57	110.88
Coral rock	4.11	3.26	1.87	1.27	138	65.74
Consolidated rubble	4.19	3.20	2.66	2.06	21	67.05
In situ branching colonies	3.46	4.01			13	55.38

Sizes of juvenile corals
The distribution of *Acropora* juveniles is bimodal (Fig. 11 top), the modes at 11–15 mm and 31–35 mm possibly corresponding to 2 years of origin. Patterns for other common genera (not shown) are less distinct: *Montipora* appears to be trimodal, with peaks in the 6–10 mm, 16–20 mm, and 31–35 mm classes, while *Pavona* appears to have 4 modes: with 6–10 mm, 21–25 mm, 31–35 mm, and 46–50 mm classes.

Colony diameters of 172 living *Acropora humilis* and 170 *A. palifera* were measured in shallow water, these 2 species previously being extremely abundant and important in such sites (Fig. 11, bottom). Both show unimodal distributions in this size range.

Between atoll comparisons
The huge Great Chagos Bank has significantly lower densities of live juveniles than any other atoll (average 3.06 juveniles quadrat^{-1}, σ = 3.66, n = 71, compared with mean: 4.59–6.38; σ = 2.80–5.65, n = 13–48, in other atolls). There were no significant differences between any of the other atolls. There appeared to be no fewer dead *Acropora* tables available, so new coral recruitment in the Great Chagos Bank is clearly lower than in other atolls.

Other groups on dead tables
A third of table surfaces supported live biota, mainly red algae (Fig. 10). *Acropora* juveniles occupied 4%, as did soft corals. All other corals occupied 2%, and sponges were conspicuous also. The advantage of examining *in situ* tables is that they offer a substrate which became available at the same time, without previously colonizing organisms to confound the picture. Colonization is high compared with that on the substrate on which they stand (which is largely dead corals of other genera), presumably because the elevation avoids erosive action from mobile rubble. However, the table habitat is temporary. In many locations they have already disintegrated and disappeared, leaving only stumps as evidence of their former abundance (13). At sites where tables survive, they are fraying and weakening, so survival of these coral recruits is uncertain.

Nevertheless, coral recruitment to small size is high. Comparisons with other locations are complicated by the minimum sizes of juveniles recorded by different surveys, because very small corals (1–5 mm diameter) dominate the population. Initial recovery in Chagos may be better than on Heron Island in the Great Barrier Reef (mortality from different causes) where up to 12.71 new recruits m^{-2} yr^{-1} were recorded (20). With an adjustment because the present survey sampled 2 yrs' recruitment, an equivalent Heron Island sample might have been about 25 juvenile corals m^{-2}, or a third of that found at Chagos. However, if the Chagos survey had sampled a minimum size of, say, 20 mm, the numbers recorded would have been equivalent between sites. Other data show lower recruitment in the Maldives and Seychelles (21, 22). High initial numbers of small juveniles decline exponentially with time (23), and arguably recruit-

ment to a size large enough to reproduce is the only kind that matters. Thus, these recruits indicate *potential* recruitment only, and it is too soon to determine recruitment *per se*. *Acropora* recruits generally grow to 10–15 mm diameter in their first year (24), and to 30–50 mm diameter by their second. A cohort of third year recruits (around 60 mm in diameter) is largely absent, indicating that spawning in late 1998 was significantly reduced, as might be expected. Other genera show a similar pattern, which is evidence for a clear annual recruitment pulse, remarkable perhaps in a location with only a 3°C annual temperature cycle.

Reef fish populations
For comparison with 1996 data, fish responses were studied largely at 15 m depth, although for the northern atolls this lies a little below the most affected depth. Examination of reef substrate (Fig. 12) focussed on the habitat from the viewpoint of providing resources to fishes. Here, for example, dead corals are categorized from the point of view of the fine covering of 'turf algae' they offer. Dramatic changes with widescale loss of live coral cover and correspondingly large increases of algal turf and coralline algae are confirmed. The slightly higher coral cover estimates arise because these data are from 15 m depth, where coral cover was higher in northern atolls. Lagoon bommies in Peros Banhos atoll showed perhaps the most dramatic losses of coral cover of any site.

Figure 11. Size frequency distribution of *Acropora* juveniles. Top: all species of this genus. Bottom: distribution of juveniles of the 2 very important shallow water *Acropora humilis* and *A. palifera*. Note different scales on x-axes.
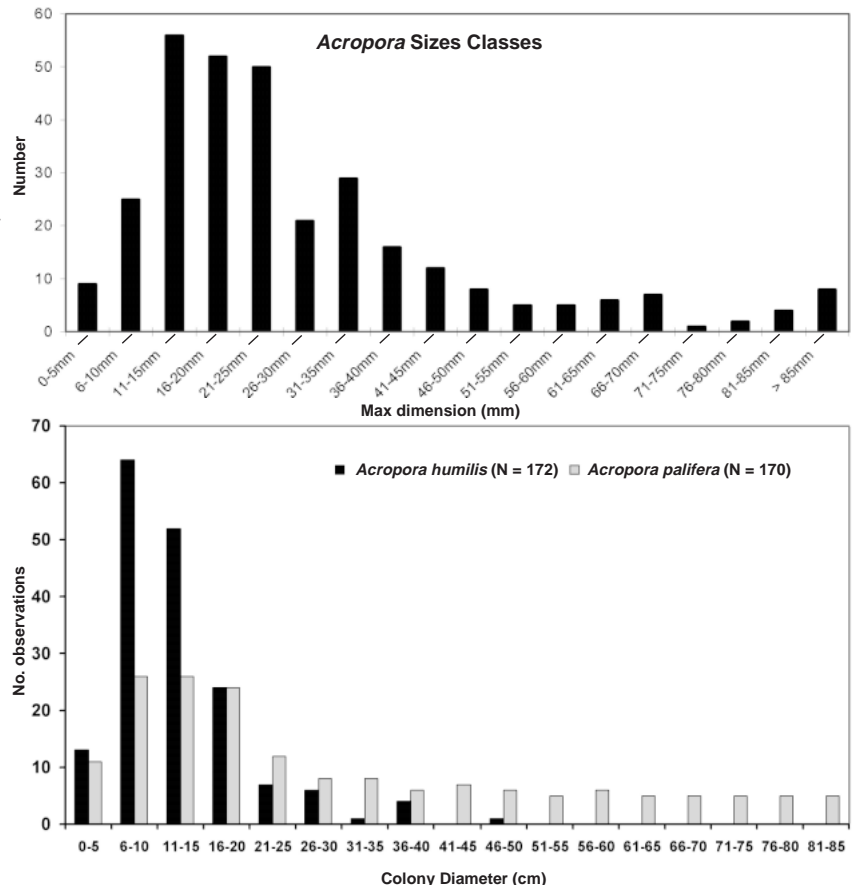
Diversity and abundance of fish species from some 203 species or groups from 29 families were analyzed (Table 4); a total of 171 species was recorded in 1996, and 165 in 2001. Overall there are no dramatic changes in abundance or diversity. The number of species observed at each site has declined in all sites in 2001, but mostly the drop is not large. There are considerable fluctuations in numbers of individuals observed, but these are heavily influenced by schooling species.

Trophic groups
Figure 13 summarizes changes in fish abundance of 9 major trophic groups. There are few clear and directed changes. Overall, corallivores have declined in abundance at some sites. Herbivores appear to have increased overall, as might be expected from the increase in algal turf. Detritivores have also increased. These often feed opportunistically on noncoral surfaces. A more detailed investigation of responses of the more numerous and well-sampled species showed that out of a total of 233 tests, some 100 showed a significant change in fish populations (Type I errors would be likely to account for only about 12 falsely significant findings). Corallivores are few, though *Chaetodon trifascialis*, and *Labrichthys unilineatus* showed significant declines ($p < 0.05$ in all site level tests). Most other corallivores showed declines although these did not test as significant. 'Coral nestlers', small fishes which shelter in corals, all showed declines, 3 out of 5 tests being significant. The 2 species of hawkfish showed significant declines; these small ambush predators tend to lie in wait on live coral and thus the loss of this habitat may have reduced their hunting success. Increases in herbivores were seen in several species. The numbers of large changes are greater in sites with the greatest loss of coral cover, and this was most marked in lagoon bommie populations. Few other groups showed directed changes, although the large increases in abundance of several schooling species of planktivores at some sites is notable.

These changes are supported by the semiquantitative abundance data. The northern Great Chagos Bank (Nelson Island reefs) had suffered very large loss of coral and showed greatest declines in corallivores, coral nestlers and hawkfishes, and an increase in many herbivores.

Stability of the reef fish populations
Other than described, reef fishes have remained remarkably unaffected thus far at 15 m depth. This parallels observations in the southern Seychelles in 1999, one year after the bleaching event, and on the Great Barrier Reef following a 55–90% coral mortality following a crown-of-thorns starfish infestation (25). It would appear that reef fish are highly resilient to changes in the benthic substrate cover in the short term, or else other factors may be more important in influencing coral reef fish community structure. As erosion continues, much larger-scale changes to the complexity of the reef surface may occur. This has devastated reef fish populations in other areas (26). What will be critical here is whether sufficient new growth can occur in time to counter the erosion.

DISCUSSION

Changes in Reef Community Structure

Disintegration of coral colonies has advanced quickly since 1998, with most dead colonies now lacking distinguishing features. Table corals remain recognizable, though about half have disappeared. Erosion of fragments is extensive and dense shallow thickets of wave-breaking *Acropora* have disappeared. Susceptibility to raised temperature differs between species (27), but the important branching corals are most susceptible. Changes in dominance patterns may develop (24, 28).

In attempting to find corollaries from elsewhere, the only such event associated with bleaching was a mass-mortality of corals in 1982–1983 in the eastern Pacific (29). However, those reefs have an unusual ecology, and may not be comparable. Ecosystem-wide impacts have been seen following plague infestations

Figure 12. Summaries of substrate cover from 1996 (top row) and 2001 (bottom row) conducted for fish study. Figures for the northern atolls are combined from 3 outer slope locations. Clear declines in both hard and soft coral cover are notable at all sites, but most particularly in the Peros Banhos Lagoon and Eagle Island (Great Chagos Bank) sites. BR - branching coral, MC - massive coral, EN - encrusting coral, SC - soft coral, AL - algal turf, MA - macroalgae, CA - coralline algae, SA - sand, RU - rubble, RK - bare rock.
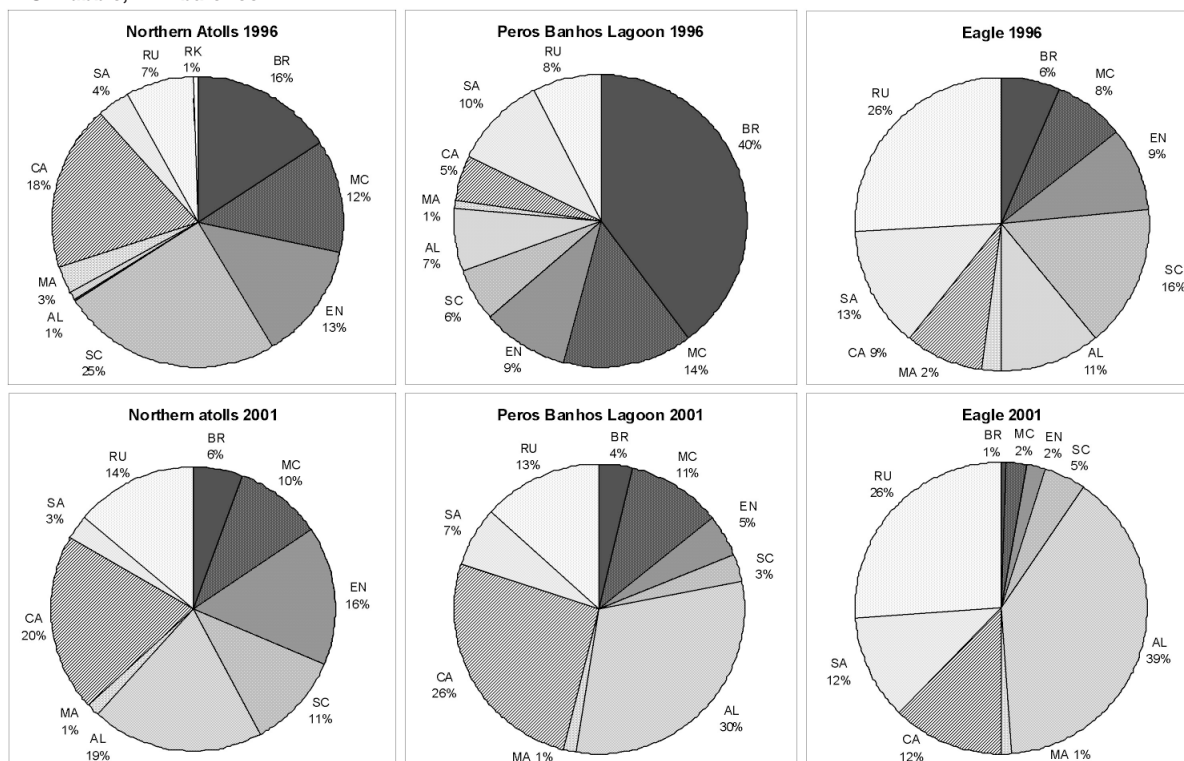
Table 4. Summary of the findings in terms of overall abundance and diversity of reef fishes in 1996 and 2001. Note that the numbers of censuses undertaken at all sites in Perhos Banhos were higher in 1996 and hence the species totals for these may not be directly comparable. The large influence of schooling species on the total number of individuals seen per count is reflected in the considerable variance in the numbers of individuals per count.

	Salomon		Peros Banhos SW		Peros Banhos NW		Peros Banhos Lagoon		Eagle, Great Chagos Bank	
	1996	2001	1996	2001	1996	2001	1996	2001	1996	2001
Total spp.	108	89	103	95	106	102	91	83	103	100
Mean spp per count	45.7	43.8	47.1	50.2	48.3	50.5	46	46	49.2	43.8
S.D.	7.5	4.8	4.2	5.9	6.1	5.7	5.8	3.8	7.5	2.2
Mean indiv count^{-1}	732	794	668	1313	654	1338	613	273	509	1085
S.D.	336	442	268	483	360	569	395	101	109	816

by crown-of-thorns starfish which feed on corals (25, 26, 30). Recovery is at best very slow.

Impacts on fishes over the short term are related to changes in availability of food or shelter (31, 32). After only 3 yrs it is perhaps not surprising that coral reef fish abundance is not affected for many groups. Subsequent changes are difficult to predict. It is highly likely that there will be further changes in the dominance of particular species, particularly if macroalgae colonize extensively (32–34). The physical reef matrix structure is critical for the maintenance of diversity and abundance. Such a structure was observed to break down following a crown-of-thorns starfish infestation in Japan (26) leading to a collapse in fish abundance and diversity. If new, or algal dominated systems become established, changes may become both marked and stable.

Diego Garcia is the southernmost atoll, and is inhabited. Visited sites on the western outer reef slope showed some of the lowest coral cover of all, to 30–35-m depth, with advanced degradation of dead corals and high rates of bioerosion. Coral recruitment is occurring, but the rapid loss of dead coral structures may have wider implications at least for several years, until new recruits reach high levels of surface cover and can reverse any net loss of reef.

The Great Chagos Bank is the largest atoll structure in the world (35), and supports small islands with particularly high biotic value due to their seabirds and hardwood vegetation (14). These reefs showed some of the lowest coral cover of all, bioerosion was high, and of particular concern also was its low coral recruitment. This may be related to distance from surviving adult populations, or perhaps greater warming and heat retention by its huge lagoon. Its fish communities were also impacted more than other sites.

The northern atolls of Salomon, Peros Banhos, and Blenheim presented a puzzling pattern. They were amongst the worst affected in water to 5 m depth, where previously near-total cover of *Acropora palifera* on western and northwestern sides was virtually eliminated. But they were least affected below 10-15 m. Coral recruitment was relatively high, and rubble pieces were larger, indicating slower bioerosion, or less physical breakdown or export.

Future change
At present, erosion is clearly a potential problem. Given the small size of new corals, erosion clearly is currently 'winning'. The balance may tip in favor of growth after further disintegration of the mobile rubble reduces it to finer particles which then are

Figure 13. Summaries of fish abundance, summarized by major trophic groups. 1996 data shown in grey bars, 2001 data in black. Sal – Salomon, PBSW – Peros Banhos South-West, PBNW – Peros Banhos North-West, PB Lag – Peros Banhos lagoon bommies, Eagle – Eagle Island (Great Chagos Bank).
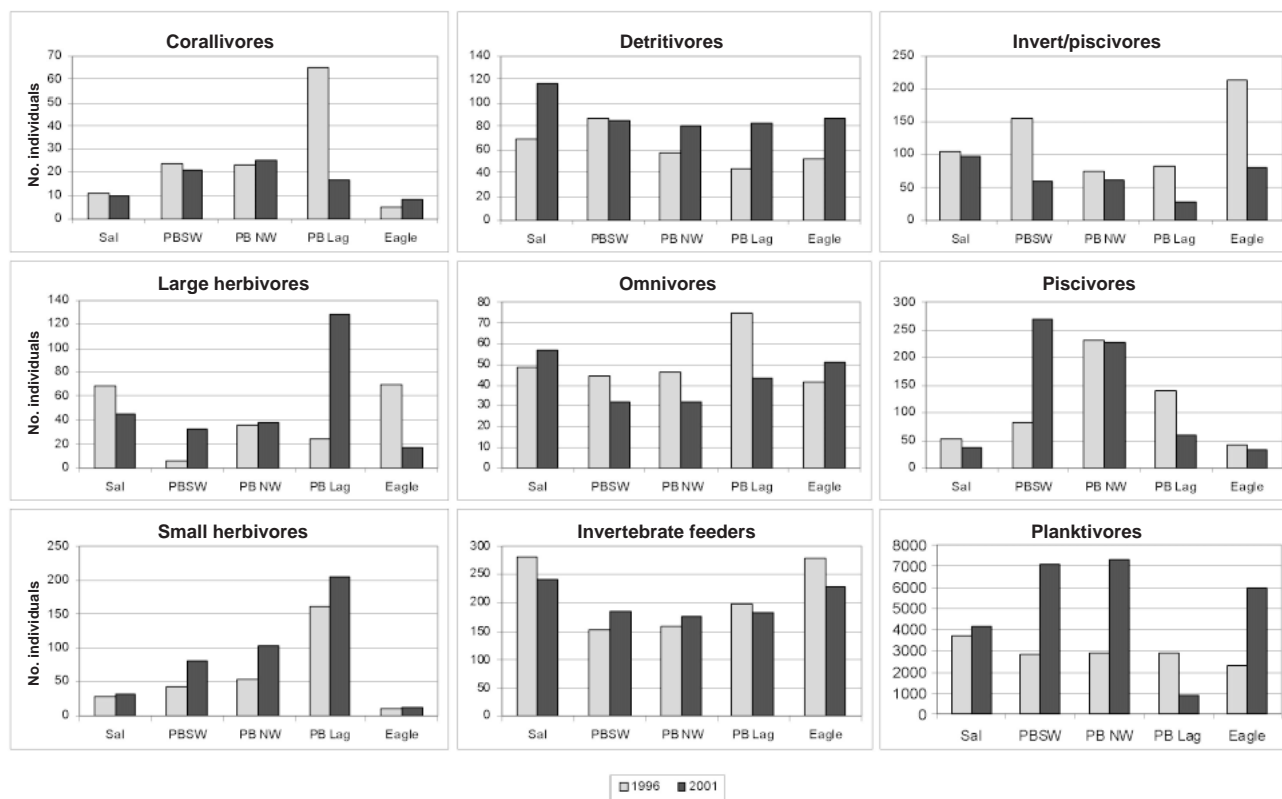
carried away, leaving greater proportions of firm substrate for new coral attachment.

Stocks of surviving adult corals in deeper water in the north point to the importance and conservation value of those locations which survived best in 1998. It is also widely known that recovery is more secure, and more rapid, on reefs not heavily impacted by other stresses like pollution and overfishing, and which have not become swamped with algae due to nutrient enrichment. The visual result now in shallow sites which have degraded the most is not dissimilar to the aftermath of dynamite fishing on reefs, from which recovery takes decades, or is predicted not to be possible at all (36). However, Chagos has one of the least stressed reef systems in the world in terms of direct human impacts (14), and because it has escaped most stresses,

Chagos perhaps stands a better chance than most places for eventual recovery. In the meantime, if processes of net erosion continue, if only for a few years, there could be serious implications for coastal erosion and loss of island area, including those with valuable infrastructure. Long-term conservation plans in this respect must obviously also focus on sustaining the least affected areas.

Over the next few years and decades it is likely that coral mortality events will recur. The temperature trends illustrate the point, and SST in April 2001 reached to within 1°C of the very damaging 1998 level. This being the case, the fine balance between reef growth and erosion could yet be lost, and there may be more widespread problems of erosion throughout the archipelago.

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37. We gratefully acknowledge funding provided by the British Indian Ocean Territory Administration. Many people were of enormous help while we were in the field. We are most grateful to the British Representative, Cdr. Peter Lewis, who extended his help copiously and willingly, Captain Rob Edye and his team of Royal Marines who provided all the small boat help we could possibly need or use, and the skipper of the Fisheries Patrol Vessel, Bob Goodwyn and his crew, with the Fisheries Officer, Andy Watson, all of whom provided substantial help most willingly. John Topp, the Conservation Adviser for BIOT, likewise continued to offer numerous helpful suggestions. To these and others unnamed, we are most grateful.
38. First submitted 25 July 2001. Accepted for publication after revision 15 October 2001.

Charles Sheppard is a tropical marine ecologist working in pollution and conservation issues, particularly those of coral reefs and associated habitats. He was scientific leader of several expeditions to the Chagos Archipelago from 1975 to the present, and a long term aim is to develop methods which help distinguish natural from anthropogenic effects on marine systems. His address: Department of Biological Sciences, University of Warwick, Coventry, CV4 7AL, UK.
E-mail: csheppard@bio.warwick.ac.uk

Mark Spalding is the senior marine ecologist at the UNEP World Conservation Monitoring Centre and is also a research associate in the Cambridge Coastal Research Unit, University of Cambridge. He has undertaken fieldwork on reef fish in Chagos and the Seychelles for a number of years, but also works globally on reef mapping and assessment and recently completed the World Atlas of Coral Reefs. His address: WCMC, 219 Huntingdon Road, Cambridge CB3 0OL, UK.
E-mail: mark.spalding@unep-wcmc.org

Simon Wilson works as a consultant specializing in coral-reef management issues and is also a post-graduate student at Warwick University. His research relates to the response of corals and reefs to the marginal environmental conditions in Southern Arabia. His address: PO Box 2531, CPO 111, Seeb, Sultanate of Oman.
E-mail: 106422.2221@compuserve.com.

Clare Bradshaw has worked on coral reef erosion and bioerosion of corals in the Seychelles, and more lately on fisheries related issues. Her address: Port Erin Marine Laboratory, University of Liverpool, Isle of Man, IM9 6JA, UK.
E-mail: cbrads88@hotmail.com